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**NEW RODENTS FROM THE LOWER MIOCENE
GERING FORMATION OF WESTERN NEBRASKA**

By

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The lower Miocene Gering Formation of northwestern Nebraska was deposited during a time of important modifications in the composition of the North American mammalian fauna. The base of the Gering Formation marks a change from dominantly eolian deposition, typical of arid conditions, to channel and floodplain deposition in broad river valleys, indicating a more mesic climate. A number of characteristically Oligocene mammals make their last known appearance in North America during the time of deposition of the Gering Formation. These include *Nanodelphys*, *Geolabis*, *Proterix*, *Eumys*, and *Hyaenodon* (Martin, 1973). Simultaneously, a number of Eurasian genera, including *Amphechinus*, *Plesiosminthus*, and *Menoceras*, first appear in North America.

Only a small fraction of the fauna of the Gering Formation has been noted in print. Reported forms include a canid *Sunkahe-tanka geringensis*, the scimitar-toothed felid *Nimravus*, the oreodonts, and the cricetid rodent *Paciculus* (Barbour and Schultz, 1935; Toohey, 1959; Schultz and Falkenbach, 1949, 1954, 1968; Alker, 1969). This paper adds to the rodents from the Gering fauna a new genus and species of phiomyid-like rodent, a new species of sicistine, and a new geomyid.

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¹ Museum of Natural History, and Department of Systematics and Ecology, The University of Kansas.

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FAUNAL AND AGE RELATIONSHIPS

The Gering Formation is composed of channel sands and flood-plain silts deposited in an ancient valley system, and is best exposed along Wildcat Ridge and Pine Ridge in western Nebraska, where it has maximum thickness of about 200 feet. In terms of the European Standard, the Gering fauna seems to correlate best with part of the fauna from the continental Aquitanian. In North America, the Gering fauna correlates almost exactly with that from the upper portion of the Sharps formation in South Dakota as reported in detail by Macdonald (1963, 1970). The Gering fauna is also, in part, correlative with the "Lower Harrison" fauna from Wyoming. Portions of the Cabbage Patch beds in Montana and the John Day beds in Oregon are probably very close to Gering time equivalents. In Nebraska, the Gering Formation is the lowest formation in the Arikaree Group and the base of the Gering may lie near the boundary between the Oligocene and Miocene epochs. The age of the lower Gering may be near 28-29 million years B.P. (Obradovich, Izett, and Naeser, 1973). The lower boundary, with the Oligocene Brule Formation, is variable and may be an erosional unconformity or in a few places an ancient soil profile, the Bayard Paleosoil (Schultz and Stout, 1955:46). Both the Sharps Formation and the Gering Formation have a gradational contact with the Monroe Creek Formation. In Nebraska, this boundary is characterized by the presence of abundant "pipey concretions" in the Monroe Creek Formation and their absence or rarity in the Gering Formation (Schultz, 1941).

The collection of small mammal faunas from the early Miocene Sharps Formation of South Dakota and the Gering Formation of Nebraska provides us with critical new information about faunal exchanges and the early radiation of several rodent families including the aplodontids, cricetids, and geomyids. Known faunal relationships show that the Sharps covers a greater time span than does the Gering (Martin, 1973). The lower Sharps and the upper Sharps are not known to occur together at any single section. Lithologically the lower Sharps resembles the Whitney Member of the Brule Formation, and contains more primitive animals than

are found in the lower Gering. This is especially evident in the beavers and lagomorphs. The Sharps also contains a number of typically Oligocene mammals that are not known to occur in the Gering of Nebraska, such as *Hyracodon*, *Leptochoerus*, and *Scotimus*. It is possible that the lower Sharps is really late Oligocene (Whitneyan). A small vertebrate fauna from a channel deposit discovered by J. C. Harksen (KU S.D. 16 in Sec. 1 and 2, T. 11 S., R. 9 E., Fall River County, South Dakota) gives us an insight into the lower Sharps fauna. It includes: *Trimylus*, *Domnina*, *Proterix*, *Geolabis*, *Ictops*, *Proscalops*, *Arctoryctes*, *Sinclairiella* cf. *dakotensis*, *Palaeolagus hypsodus*, *Palaeolagus philoi*, *Prosciurus* sp., *Pelecomys* sp., ?*Allomys* sp., *Haplomys* sp., ?*Meniscomys* sp., tree squirrel, *Protosciurus*, *Protospermophilus*, *Miospermophilus*, *Agnotocastor*, *Eutypomys*, small eomyid, *Paradjiaumo*, "*Paciculus*" cf. *mcgregori*, *Leidymys* cf. *blacki*, *Eumys brachyodus*, *Scotimus* cf. *kellamorum*, *Heliscomys*, *Proheteromys*, *Tenudomys*, *Florentiamys*, *Leptochoerus*, *Hypisodus*, and *Leptomeryx*.

This fauna (Blue Ash Local Fauna) contains many forms transitional from those of the Middle Oligocene to those of the Gering. Its main importance is that it may give us a glimpse of a mesic small mammal fauna during Whitneyan times. It is interesting that it contains *Ictops* and eomyids while at the same time lacks the immigrant genera *Amphelchinus* and *Plesiosminthus*.

SYSTEMATIC ACCOUNTS

CLASS MAMMALIA Linnaeus, 1758

ORDER RODENTIA Bowdich, 1821

SUPERFAMILY GEOMYOIDEA Weber, 1904

FAMILY GEOMYIDAE Gill, 1872

Tenudomys Rensberger, 1973

Tenudomys titanus, new species

Figure 1

Holotype.—University of Nebraska State Museum 11531, left P¹.

Type locality.—UNSM Mo-119, Durnal locality, NW $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 32, T. 20N., R. 52W., $\frac{1}{2}$ mile southwest of UNSM Mo-110, 6 $\frac{1}{2}$ mi. south and 1 $\frac{1}{4}$ mi. west of Bayard, Morrill County, Nebraska.

Horizon.—Helvas Canyon Member, Gering Formation, Arikaree Group, Miocene.

Referred material.—Left M¹ or M², UNSM 11504. From the same locality and horizon as the type.

Diagnosis.—Larger and more brachydont than any other *Tenudomys* or *Pleurolicus*; protoloph consisting of a single major cusp on P¹; P¹ without cingula.

Etymology.—*Titanus*, Greek *Titan*, symbolic of large size.

Description.—P¹ very large, brachydont, and cusped, lacking cingula, protoloph consisting of a single antero-posteriorly compressed cusp, with

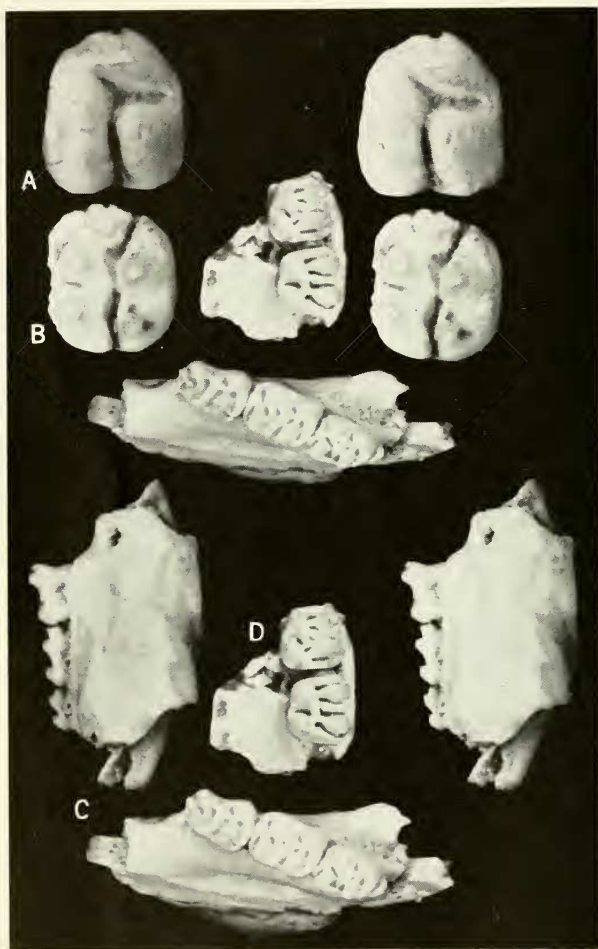


FIG. 1.—*Tenudomys titanus*, occlusal views: A. UNSM 11531 (holotype), left p^4 ; B. UNSM 11504, left M^1 or M^2 . *Plesiosminthus geringensis*: C. UNSM 11708 (holotype), partial right ramus with M_{1-3} , labial and occlusal views; D. UNSM 11519, partial right maxilla with M^{1-2} . All $\times 10$.

metacone and hypocone well separated on metaloph, entostyle cuspidate and continuous with metaloph; M^1 or M^2 with a slight posterolabial cingulum ending in a small entostyle, protoloph consisting of small protostyle, protocone, and paracone, metaloph with metacone and hypocone, and medial valley straight.

Discussion.—The P^4 resembles most closely that of *Tenudomys dakotensis* (Macdonald) from the Sharps Formation, but is about 60 per cent larger than the P^4 in that species. The P^4 of *Tenudomys titanus* can be distinguished from that of *Florentiamys* by the lack of an anterior cingulum and from *Sanctimus* by having a single elongated anterior cusp rather than a distinct paracone and protocone united only at their bases (Rensberger, 1973:840). *Tenudomys titanus* can probably be derived from a smaller and more brachydont form of *Tenudomys*, which is represented by a number of isolated teeth from the ? Late Oligocene of South Dakota (Blue Ash Local Fauna). *Florentiamys* also occurs in the Blue Ash Local Fauna indicating that by the late Oligocene the major lineages of fossorial geomyid rodents had already separated from the Heteromyidae and may have been progressing towards fossorial adaption which finally made them the dominant rodents of the late Arikarean.

SUPERFAMILY DIPODOIDEA Weber, 1904

FAMILY ZAPODIDAE Coues, 1875

SUBFAMILY SICISTINAE Allen, 1901

Plesiosminthus Viret, 1926

Plesiosminthus geringensis, new species

Figure 1

Type.—UNSM 11708, partial right ramus.

Type locality.—UNSM Mo-119.

Horizon.—Helvas Canyon Member, Gering Formation, Arikaree Group, Miocene.

Referred material.—UNSM 11519, partial right maxilla with M^{1-2} and alveolus from P^4 , from the same locality and horizon as type.

Diagnosis.—Larger than *Plesiosminthus clicosus* and smaller than any other described North American sicistine; slightly larger than *P. myarion* or *P. schaubi*; anterocone absent on M^1 ; cingula indistinct; upper molars relatively square.

Etymology.—Named for the Gering Formation.

Description.—Posterior border of incisive foramina opposite P^4 ; alveolus for P^4 indicating posteriorly inclined, single-rooted tooth; upper molars not convex buccally as in *P. schaubi*, *P. myarion*, or *Parasminthus* (more similar to *Schaubeumys* in this respect); molars (especially M^1) not elongate as in European species of *Plesiosminthus*; molars without distinct cingula; molars with paracone and metacone higher than other cusps (but lower than in other North American species of *Plesiosminthus* or *Schaubeumys*); internal embayments of the molars U-shaped as in *Schaubeumys* (Wilson, 1960:84); M^1 with anteroloph almost separate from paracone, paracone straight and joining

protocone, paracone and protocone joined directly by protoloph, anterocone absent, endoloph connecting protoloph with hypocone, low mesoloph extending from endoloph to buccal border of tooth and joining a small mesostyle, hypocone with thin connection (metaloph) with metacone, posteroloph extending from hypocone to buccal margin of tooth; M^2 with anterior half of tooth wider than posterior, anteroloph isolated from paracone and connecting with very small anterocone before joining protocone, protoloph extending from anteroloph to paracone, mesoloph low, short and not connecting with mesostyle (although it does have a broad, low connection with the metaloph), metaloph arising from endoloph and connecting with metacone, posteroloph connecting with hypocone and shorter than in M^1 ; ramus small with mental foramen high (about as in *Plesiosminthus clivosus*); dorsal and ventral masseteric lines meeting slightly posteroventral to mental foramen with ventral line extending a short distance further anteriorly; small foramen present between M_2 and ascending ramus as is found in *P. clivosus*; lower incisor narrow with smooth enamel; M_1 more elongate than in *P. clivosus* with talonid much wider than trigonid, large anteroconid median and double, connected by anterior mure to metaconid, protoconid and metaconid low, about same size and connected by metalophid, ectolophid low and with a large mesoconid leading into a mesolophid ending in mesostylid on lingual border of tooth, mesostylid connected to prominent posterior cingulum; M_2 like M_1 except with anteroconid small and single and trigonid and talonid nearly same width; M_3 much like M_2 ; lingual and buccal cingula not developed on lower molars.

Discussion.—*Plesiosminthus geringensis* is the oldest and one of the smallest known North American sicistines. It is referred to *Plesiosminthus* rather than to *Schaubeumys* on the basis of its lack of distinct cingula (very slight cingula are present on the buccal and lingual anterior margins of the upper molars), low paracone and metacone, and the relative proportions of M_2 (anterior end wider than posterior). Because the upper incisors of the new species are unknown, it is impossible to tell if they were grooved as in *Plesiosminthus* or ungrooved as in *Parasminthus*. The cheek tooth pattern of *Plesiosminthus geringensis* is very similar to that of some specimens of *Parasminthus* illustrated by Bohlin (1946; plate 1); however, the paracone and metacone seem higher in the illustrations of the Asian genus (possibly an artifact of the stereophotographs). *Plesiosminthus geringensis* is smaller than any of the species of *Parasminthus* described by Bohlin.

The earliest known sicistines are from the Upper Oligocene of Europe and Asia. Sicistines are presently unknown from the Oligocene of North America and it seems reasonable to suppose that *Plesiosminthus geringensis* is an immigrant from Eurasia. However, we must not ignore the ecological bias in our collecting. Especially important with sicistines is the almost complete lack of mesic faunas from the Upper Oligocene of the Great Plains.

SUPERFAMILY indet.

Zetamys, new genus

Type species.—*Zetamys nebraskensis*, new species.

Diagnosis.—Near the size of a rat, *Rattus rattus*; cheek teeth lophate and

moderately hypsodont; p^4 molariform; tooth pattern consisting of an anterior transverse crest and a posterior "V" forming a distinct "Z" pattern; length/width ratio of molars less than in most North American eomyids (tending to be nearly square); distinct cingula absent.

Etymology.—*Zeta*, Greek, Z; *Mys*, Greek, mouse.

Zetamys nebraskensis, new species

Figures 2 and 3

Holotype.—UNSM 11514, right P^1-M^1 .

Type locality.—UNSM Mo-104, Roundhouse Rock, SW $\frac{1}{4}$, Sec. 21; W edge, SE $\frac{1}{4}$, Sec. 21. T. 19N, R. 51W, 4 $\frac{1}{2}$ mi. south and 5 $\frac{1}{2}$ mi. west of Bridgeport, Morrill County, Nebraska.

Horizon.—Helvas Canyon (lower) Member, Gering Formation, Arikaree Group, Miocene.

Referred material.—Two partial left rami with M_{1-3} , UNSM 11566 and 11567; three left P 's, UNSM 11720, 11574, and 11565; one right P , UNSM 11568; one right M^2 , UNSM 11569; one left M^2 , UNSM 11718; and a partial right M^3 , UNSM 11719. All from same locality and horizon as type.

Diagnosis.—Cheek teeth moderately hypsodont with a prominent "Z" pattern; p^4 molariform with anteroloph connected to paracone.

Etymology.—Named for the State of Nebraska.

Description.— P^1 consisting of an anterior crest composed of "tear-shaped" protocone uniting buccally with anteriorly-arched anteroloph connecting to paracone through small protoconule, two posterior lophs forming a "V" with the hypocone at its apex (longest of these lophs running from paracone to hypocone), posterior loph of "V" running from hypocone to metacone and connecting to short posteroloph at about mid-line of tooth, lingual end of anterior crest projecting posteriorly and buccal end of posterior crest projecting anteriorly forming basin-like lingual and buccal valleys; M^{1-2} essentially like premolar except with anteroloph less arched and protoconule not evident as separate cusp; M^2 slightly larger than M^1 ; M^3 represented by partial tooth (UNSM 11719) missing anteroloph, lophs forming posterior "V" parallel to

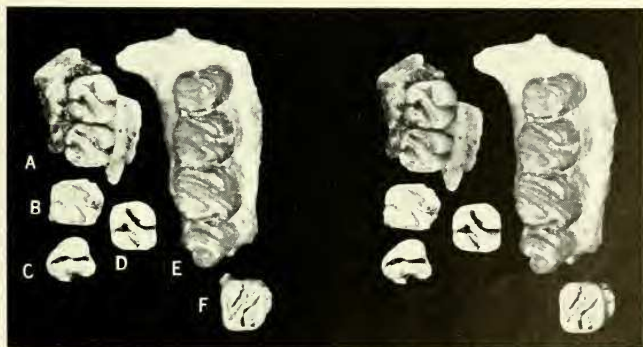


FIG. 2.—*Zetamys nebraskensis*: A. UNSM 11514 (holotype), right P^1-M^1 ; B. UNSM 11720, right M^2 ; C. UNSM 11719, partial right M^3 . D. *Zetamys* sp., KU 19001, right P^1 ; E. *Gaudcamnus aegyptius*, YPM 18004, right maxillary with P^1-M^1 ; F. *Zetamys* sp., KU 19002, right M^1 . All occlusal views, $\times 5$.

each other, arched posteriorly and equal in length, two small buccal roots and two larger fused lingual roots on upper cheek teeth; upper and lower teeth have no cingula separate from lophs; P_4 submolariform with anterior half narrower than posterior part of tooth, protoconid connected to metaconid by short transverse anterior loph and to entoconid by long diagonal loph which may have short buccal loph near its midpoint, hypoconid forming buccal margin of posterolophid which is connected to entoconid by narrow enamel band; M_{1-2} similar to premolar except that they are more rectangular and with anterolophid longer; M_3 not recognized in the material studied.

Discussion.—The “Z” pattern found in the cheek teeth of rodents has developed independently in a number of different groups, including the Phiomysidae (*Gaudeamus*), the Caviomorpha (*Plagiodontia*), and the Eomyidae (*Rhodanomys*). The total amount of crested surface has not been increased in these genera and may be reduced from an earlier condition through the loss of transverse crests (mesoloph, posteroloph, etc.). For instance, a lower first molar of *Gaudeamus aegyptius* has only about 57 per cent as much development of crests as on the comparable tooth in *Metaphiomys schaubi* (if their teeth are scaled to the same size and the total length of all the crests is measured). This suggests that selection is acting on the arrangement of the transverse crests, rather than for addition or length of crests. The direction of change seems to be towards a diagonal arrangement which is best typified by *Plagiodontia*. In the terminology of Hershkovitz (1962) the teeth of these rodents, with “Z” tooth patterns, have undergone progressive planation, hypsodonty, and involution. Development of these features may indicate that these animals consume abrasive or fibrous foods, although some hypsodonty may be developed to compensate for the loss of crested surfaces.

Zetamys seems to provide an example of parallelism. The molar teeth of this genus correspond in almost every detail (they are slightly smaller) to the molar teeth of the early Oligocene phiomysid *Gaudeamus* from the Fayum basin in Egypt (figures 1 and 3). The cheek teeth of *Gaudeamus* are more brachydont and the premolars less molariform than in *Zetamys*. *Zetamys* might reasonably be considered related to *Gaudeamus*. However, none of the critical features found in phiomysids, including the size of the infraorbital foramen, the shape of the ramus, or the nature of the incisor enamel, is known for *Zetamys*. The European comysid *Rhodanomys* has a fundamentally similar tooth pattern. In *Rhodanomys*, the anteroloph may be isolated from the ectoloph, which combines with the protoloph to form a single long transverse crest. To further convert the teeth of *Rhodanomys* to the pattern found in *Zetamys*, it would be necessary to move the metaloph posteriorly and reduce the posteroloph to a small crest, arising from the metaloph at approximately the midline of the tooth. The small buccal loph which sometimes comes off the long loph between the para-

cone and the hypocone may then be a remnant of the mesoloph.

On the lower cheek teeth the anterior crest may actually correspond to the metalophid in *Rhodanomys* as this crest runs from the metaconid to the protoconid. In *Rhodanomys*, there is a small anteroloph in front of the metalophid. In both *Rhodanomys* and *Zetamys* the mesolophid is vestigial or absent and the ectolophid combines with the hypolophid to form a loph extending from the protoconid to the entoconid. The hypoconid is isolated from this long transverse loph and is continuous with the posterolophid forming the posterior border of the tooth.

The ancestry of *Zetamys* seems doubtful. It is not similar enough to *Rhodanomys* to indicate a close relationship to that genus, but the possibility that it is a Eurasian immigrant should not be discounted. *Zetamys* shows no close similarity with any known North American eomyid, although Black (1965:40) does compare *Aulolithomys* from the lower Oligocene of Montana to *Rhodanomys*. However, the morphological changes necessary to convert *Aulolithomys* to *Zetamys* are very great and no real relationship can presently be suggested. The possibility that it is really a phiomysid also cannot be excluded.

Zetamys sp.

Figure 2

Referred material.—Right P⁴, KU 19001, right M¹, KU 19002, and a fragment of a right M¹ or M², KU 19003.

Locality.—KU S.D. 16 (Blue Ash Locality), S. ½, Sec. 1, T. 11S., R. 9E., Fall River County, South Dakota.

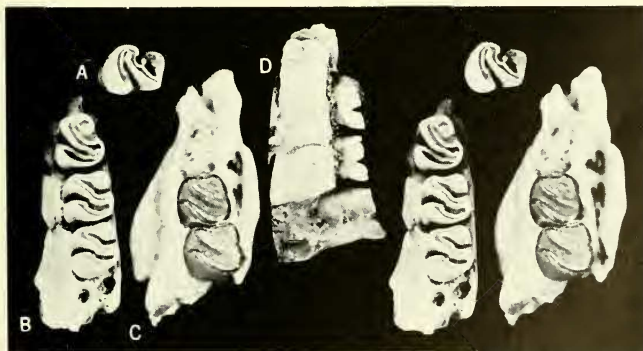


FIG. 3.—*Zetamys nebraskensis*, occlusal views: A. UNSM 11720, left P⁴; B. UNSM 11574 and 11566, left P¹ and M₁₋₂; *Gaudencamus aegyptius*, YPM 18036, left M₁₋₂, occlusal view; D. *Zetamys nebraskensis*, UNSM 11574 and 11566, left P₄ and M₁₋₂, lingual view. All × 5.

Horizon.—From ant hills, ?Upper Oligocene.

Diagnosis.—Slightly larger and less hypsodont than *Z. nebraskensis*; P¹ less molariform than in that species and with anteroloph well separated from the paracone.

Description.—The unworn P¹ is nearly square with protocone a lophate cusp, isolated from paracone by a deep groove (valley), crests from paracone and metacone forming "V," with hypocone at its apex, posteroloph absent; M¹ or M² with a "V" formed as in premolar except that a small buccal loph occurs near middle of loph between paracone and hypocone; upper molar tooth fragment (KU 19003) contributes no additional information.

Discussion.—This *Zetamys* is more primitive than *Z. nebraskensis*, in that it is less hypsodont and the premolar is less molariform. It is also somewhat older. Its presence in the Blue Ash Local Fauna suggests that it might occur in other Oligocene faunas.

TABLE 1.—MEASUREMENTS OF THE TEETH OF *Zetamys*, *Tenudomys*, AND *Plesiosminthus* (in mm.).

		Length	Width
<i>Zetamys nebraskensis</i>			
UNSM 11514 (holotype)	P ¹	1.55	1.70
	M ¹	1.41	1.62
UNSM 11574	P ¹	1.76	1.59
UNSM 11566	M ₁	1.73	1.72
	M ₂	1.86	1.69
UNSM 11720	P ₁	2.03	1.81
<i>Zetamys</i> sp.			
KU 19001	P ¹	1.54	1.68
KU 19002	M ¹	1.71	1.88
<i>Plesiosminthus geringensis</i>			
UNSM 11708 (holotype)	M ₁	1.20	.83
	M ₂	1.21	.97
	M ₃	.98	.81
UNSM 11519	M ¹	1.06	1.01
	M ²	1.00	1.03
<i>Tenudomys titanus</i>			
UNSM 11531 (holotype)	P ¹	2.43	2.74
UNSM 11504	M ¹ or M ²	1.90	2.22

CONCLUSIONS

The development of arid conditions during the late Oligocene may have favored the evolution of the heteromyids, as they have a major radiation at this time. They must also have given rise to the early gophers during this time, for the Gering and Sharps formations already contain fairly well-differentiated ancestors for the Geomyinae in *Sanctimus* and the Pleurolicinae in *Tenudomys*.

The sicistines appear to be Eurasian emigrants to North America, and *Plesiosminthus geringensis* is the earliest known North American form. Parris and Green (1969) have reported a sicistine from the lower Sharps but Green (personal communication, 1973)

informs me that this specimen was misidentified. The Miocene sicistines of North America tend to be cricetid-like and had their major radiation during the Hemingfordian age when cricetids were rare.

The relationships of *Zetamys* are unclear. The presence of upper and lower premolars prevent it from being a cricetid. It might be an eomyid, but it is not closely similar to any known form. It is almost identical to the Oligocene phiomyid *Gaudeamus* from Egypt. *Gaudeamus* is hystricognathus, hystricomorphus, and has multiseriate enamel on its incisors (Wood, 1968). These are features shared by hystricomorphs and caviomorphs. The presence of a form related to *Gaudeamus* in the late Oligocene and early Miocene of North America might indicate that the caviomorphs have a phiomyid ancestor but this possibility should not be considered seriously without more conclusive evidence. At the present time, *Zetamys* is best regarded, with some reservation, as an example of parallelism.

SUMMARY

A new species of geomyid, *Tenudomys titanis*, is described and represents one of the earliest occurrences of pleurolicine gophers. A new sicistine, *Plesiosminthus geringensis*, is also described and is the oldest and most primitive sicistine known from North America. *Zetamys* is a new genus of rodent from the ? late Oligocene and early Miocene of the Central Great Plains. It shows striking similarities to the African Oligocene phiomyid, *Gaudeamus*, but is probably best not referred to any family.

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